8. *On the Lancelets of South and East Africa.* By J. E. Webb, Department of Zoology, University College, Ibadan. (With five tables and three figures in the text.)

Introduction

Lancelets of the genus *Branchiostoma* have been recorded from a number of localities along the coast of the Cape Province, on the East African and Arabian coasts and in Madagascar. In 1902 Gilchrist described *Branchiostoma capense* from specimens taken at Simons Bay, False Bay, Mossel Bay and Algoa Bay in the Cape Province and, in 1923, he described a second species, *B. bazarutense*, from the Bazaruto Islands off Portuguese East Africa. Franz (1922), examining material collected by the 'Prinz Adalbert' Expedition, reported the occurrence of both *B. belcheri* and a species of an allied genus, *Asymmetron cultellus*, at Bagamoyo opposite Zanzibar. In 1928 Prenant described specimens which he considered to be inseparable from *B. lanceolatum* taken on the north-west coast of Madagascar. Webb (1956) recorded another specimen of this species and described a new lancelet, *B. arabiae*, from material collected by the 'John Murray' Expedition in 1933. The specimen of *B. lanceolatum* and the collection of *B. arabiae* were taken in the same haul near the entrance to the Gulf of Oman. *B. arabiae* is not strictly an East African form, but it is related both to *B. bazarutense* and to *B. belcheri*.

As the recognition of species in the genus *Branchiostoma* depends chiefly on the numerical evaluation of characters often subject to considerable variation, it is natural that some controversy has arisen concerning the validity of many of the species described. Some workers consider the genus to comprise relatively few species most of which are very widely distributed (Prenant 1928, and Drach 1948), while others recognize as species a larger number of more circumscribed forms (Hubbs 1922, and Franz 1922). Apart from a difference in opinion as to what degree of differentiation should be recognized in the erection of a species, much of the difficulty arises from the shortcomings of many of the early descriptions. In these, the data given are frequently insufficient first to permit adequate comparisons with other species and, second, to enable the extent of the variation of the different characters to be assessed. A case in point involves the recognition of *B. capense* from the Cape, *B. tattersalli* from Ceylon, *B. californiense* from California and *B. elongatum* from Peru and the Galapagos Islands. Following Gilchrist's description of *B. capense*, Tattersall (1903) discussed the position of this lancelet at some length and concluded that *B. capense*, *B. californiense* and *B. elongatum* are probably varieties of one species. He reached this conclusion on the general similarity of the myotome formula and dismissed as trivial other characters such as the shape of the fins. In the same year Tattersall (1903a) examined a large collection of lancelets from the oyster beds of Ceylon and found in it a single specimen which he referred to *B. californiense*. If he considered *B. californiense* and *B. elongatum* to be the same species, however, he should have referred his Ceylon lancelet to *B. elongatum* as this species, described by Sundevall in 1852 and 1853, antedates *B. californiense* first recorded by Cooper (1868) and later described by Andrews (1893) (see also Hubbs 1922). Beebe and Tee-Van (1941) later recognized *B. elongatum* and *B. californiense* as distinct, but only on a difference of the total number of myotomes in each. Franz (1922, 1922a and 1930) followed Tattersall's lead in considering both *B. capense* and Tattersall's *B. californiense* from Ceylon as uncertain species and suggested that they may be geographical varieties of *B. elongatum*, although he had not seen Gilchrist's description of *B. capense*. *B. californiense* from California he came to recognize as distinct from *B. elongatum*. Meanwhile Hubbs (1922) took the opposite view and maintained that lancelets from so widely separated localities as the Cape, Ceylon, California and Peru, Chile and the Galapagos Islands are likely to be distinct. He therefore recognized *B. capense* and went so far as to rename Tattersall's Ceylon specimen *B. tattersalli* on little evidence other than geographical location. In 1934 Prashad described a series of specimens from Ceylon together with Tattersall's specimen as *B. gravelyi* but, as has already been indicated in a previous paper (Webb 1955), *B. gravelyi* must fall into synonymy with *B. tattersalli* which, from the myotome formula given by Prashad, appears to be a valid species distinct from *B. californiense*. Drach (1948) evidently accepts the view of Franz as *B. capense* does not appear in his list of species and *B. tattersalli* is similarly omitted, but *B. californiense* and *B. elongatum* he recognizes as distinct. The doubts concerning the validity of *B. capense*, therefore, date from Tattersall's (1903) rejection of the species on what must be considered to-day as inadequate grounds and since that time material of the Cape lancelet has never been critically examined to confirm or refute his contention. Thus a review of this lancelet and those with which it has been confused is badly needed.

The occurrence of *B. belcheri* at Bagamoyo and *B. lanceolatum* in Madagascar appears at first sight to be anomalous. *B. belcheri* is a species common in the China Seas and East Indies while *B. lanceolatum* is the European lancelet. The presence of these species on the East African coast, therefore, is of great interest, but requires confirmation. In this paper an attempt is made to clarify the systematic position of the Cape lancelet and to provide confirmation of the existence of *B. belcheri* and *B. lanceolatum* in East Africa. Dr. Keppel H. Barnard of the South African Museum has kindly lent the type specimens of *B. capense* and Professor J. H. Day of the University of Cape Town has provided a collection of lancelets from Cape Province and Portuguese East Africa made in recent years by members of his department in the course of an ecological survey of those regions. The author is grateful to Dr. Barnard and to Professor Day for their co-operation and also to the Trustees of the British Museum (Natural History) for permission to examine the collections of *B. californiense* and *B. elongatum* in that museum.

Systematic Account

Family Branchiostomidae

Branchiostoma capense Gilchrist (1902)

Material examined. The type specimens 'S.A.M. 13727, one of P.F. 722' (here designated holotype), a specimen 38 mm. in length stained and mounted on a slide; 'S.A.M. 13728' (here designated paratype) a specimen 36 mm. in length stained and mounted on a slide; 'Pieter Faure No. 4055 False Bay (Cape) 24 fathoms 1900' (here designated paratype) a specimen 43 mm. in length preserved in alcohol. These three specimens are deposited in the South African Museum, Cape Town.

The following specimens lent by Professor Day: three specimens (F.B. 1104, 22.2.47) collected in False Bay 34° 08′ S. 18° 31′ 30″ E. by D-net at 27-28 metres, bottom fine shingle; two specimens (FAL. 5. S. 22.2.52) collected in False Bay, just south of Seal Island, by rock dredge at 35 metres, bottom broken shell; three specimens (LIZ. 25. K. 11.4.54) dredged in Algoa Bay 34° 00′ 24″ S. 25° 44′ 30″ E. at 39 metres, bottom coarse sand and shell; one specimen (M.B. 71. C. 19.1.56) dredged in Mossel Bay. These specimens are deposited in the Department of Zoology, University of Cape Town.

Distribution. South coast of the Cape Province, South Africa: at Simons Bay, False Bay, Mossel Bay and Algoa Bay.

Diagnosis. In the following diagnosis counts and measurements have been made on the specimens listed above and the results examined statistically. Although these specimens do not comprise a sample taken from one locality at the same time, they are, nevertheless, so uniform that they can be treated as a single series.

1. Dorsal fin chambers number 400–440: Mean 420·9: Standard Deviation 14·67: S.D. = 3·49 per cent of the Mean.
2. Preanal fin chambers number 62–80: Mean 71·2: Standard Deviation 6·11: S.D. = 8.58 per cent of the Mean.
3. Tallest of dorsal fin chambers 4·0–6·0 times as high as broad: Mean 4·55: Standard Deviation 0·64: S.D. = 14·0 per cent of the Mean.
4. Height of dorsal fin contained 7–11 times in the depth of the body in the mid-atrial region: Mean 9·4: Standard Deviation 1·36: S.D. = 14·49 per cent of the Mean.

5. Postatrioporal region 0·38–0·43 the length of the preatrioporal region: Mean: 0·405: Standard Deviation 0·014: S.D. = 3·4 per cent of the Mean.
6. Myotomes from anterior end to atriopore 44–48: Mean 46·0: Standard Deviation 1·26: S.D. = 2·75 per cent of the Mean.
7. Myotomes from atriopore to anus 18–20: Mean 19·2: Standard Deviation 0·75: S.D. = 3·91 per cent of the Mean.
8. Myotomes posterior to anus 10–11: Mean 10·1: Standard Deviation 0·32: S.D. = 3·13 per cent of the Mean.
9. Total myotomes 73–77: Mean 75·3: Standard Deviation 1·45: S.D. = 1·92 per cent of the Mean.
10. Maximum length in sample examined 64 mm.; minimum length 36 mm.

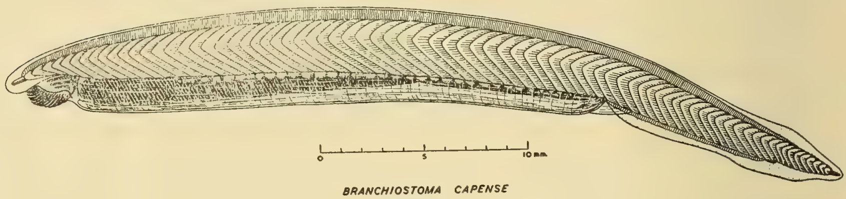


Fig. 1.

The following characters also assist in the recognition of this species and are illustrated in fig. 1 which has been prepared from *camera lucida* drawings of the holotype. The dorsal fin is approximately the same height throughout its length and is not separated from the rostrum by a post-rostral notch. The form of the rostrum and the oral region is almost identical with that of the West African species *B. nigeriense* (Webb, 1955 and 1956a). The caudal fin is also similar to that of *B. nigeriense* and in outline possesses the characteristic dorsal and ventral subterminal indentations. The preanal fin, however, differs from that of *B. nigeriense* as the fin chambers do not extend to one half the breadth of the fin. The anus lies before the centre of the lower lobe of the caudal fin.

Comparison of Branchiostoma capense *with other species of the genus*

The species with which *B. capense* is compared are selected on grounds either of similarity of structure or of occurrence in adjacent geographical locations. Thus a comparison is made with *B. californiense* and *B. elongatum* as it is with these species that *B. capense* shows similarities and has been considered synonymous in the past. *B. capense* is compared with *B. belcheri*, *B. bazarutense* and *B. arabiae* as these three species are found on the east coast of the African continent from Portuguese East Africa to Arabia. Finally a similar comparison is made with the Guinea Coast species of West Africa, *B. nigeriense*, *B. takoradii*, *B. leonense* and *B. africae*, a group near to *B. capense* both structurally and geographically. A comparison with *B. lanceolatum* which also now occurs on the east coast of Africa has not been made as the appearance of this species in the Arabian Sea and Indian Ocean is evidently very recent and the structural differences between *B. lanceolatum* and *B. capense* are considerable.

When *B. capense* is compared with *B. californiense* a number of differences are apparent which have not previously been appreciated. A single specimen of *B. californiense* from San Diego, California (B.M. reg. no. 1892.4.27.16–19), in the British Museum (Natural History) collection has been found to possess the following characteristics. The recorded range of variation in each character for this species is given in parenthesis after the figures for the specimen examined.

1. Dorsal fin chambers number 347. (312–374).
2. Preanal fin chambers number 45. (*c.* 50).
3. Tallest of dorsal fin chambers 4·0 times as high as broad. (5·0–8·0).
4. Height of the dorsal fin contained 8 times in the depth of the body in the mid-atrial region. (5–8).
5. Postatrioporal region 0·36 the length of the preatrioporal region. (0·30–0·38).
6. Myotomes from anterior end to atriopore 44. (43–48).
7. Myotomes from atriopore to anus 19. (16–19)
8. Myotomes posterior to anus 9. (8–10).
9. Total myotomes 72. (68–74).
10. Length of specimen 71 mm. (maximum length recorded elsewhere 84 mm.).

In general appearance this species resembles *B. elongatum* (see fig. 2) except that the oral cirri, although rather short, are more prominent and the dorsal fin is approximately the same height throughout the length of the body. The anus is situated behind the centre of the lower lobe of the caudal fin.

A comparison of the diagnoses for *B. capense* and *B. californiense* shows that the numbers of dorsal and preanal fin chambers are considerably higher in the former species. In *B. capense* the height of the dorsal fin tends to be relatively less than in *B. californiense* and the proportions of the dorsal fin chambers are accordingly slightly different. The relative length of the post-atrioporal region in *B. californiense* is less than in *B. capense*. In the myotome formula, while the number of myotomes before the atriopore is similar in both species, the number behind the atriopore in *B. capense* is higher so that the total myotome number is also higher than in *B. californiense*. These differences appear to be quite sufficient to indicate that *B. capense* and *B. californiense* are distinct, but, in addition, differences in the form of the rostrum, the oral region, and the caudal and preanal fins support the separation of the two forms.

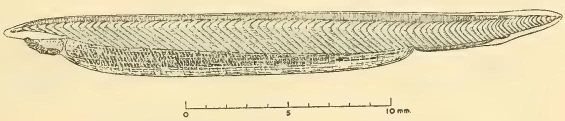
From figures recorded for *B. elongatum* by Sundevall (1852 and 1853), Snodgrass and Heller (1905), Hubbs (1922), Franz (1922, 1922a and 1930) and Beebe and Tee-Van (1941), a much higher degree of similarity in the numerical characters evidently exists between this species and *B. capense* than between *B. californiense* and the Cape lancelet. Indeed, from this published data, no clear distinction can be made between *B. capense* and *B. elongatum* and a re-examination of material of *B. elongatum* was essential before it could be determined whether, in fact, the two lancelets should be assigned to the same species. Fortunately *B. elongatum* is represented in the collections of the British Museum (Natural History) by good samples from Peru and from the Galapagos Islands. These samples have been examined and diagnoses for each are given.

Diagnosis of Branchiostoma elongatum *Sundevall* (*Peruvian sample*)

The following diagnosis is based on 16 specimens dredged from 5–8 fathoms at Lobos de Tierra, Peru, 6° 25′ S. 80° 57′ W. on 7th June 1912. They are part of a sample in the collection of the British Museum (Natural History), B.M. reg. nos. 1913.7.10.1–10. Counts and measurements have been made on these specimens and the results examined statistically.

1. Dorsal fin chambers number 350–410: Mean 381·0: Standard Deviation 18·50: S.D. = 4.86 per cent of the Mean.
2. Preanal fin chambers number 37–80: Mean 64·0: Standard Deviation 10·35: S.D. = 16·17 per cent of the Mean.
3. Tallest of dorsal fin chambers 2·7–6·0 times as high as broad: Mean 3·6: Standard Deviation 1·03: S.D. = 28·68 per cent of the Mean.
4. Height of dorsal fin contained 7–12 times in the depth of the body in the mid-atrial region: Mean 10·0: Standard Deviation 1·41: S.D. = 14·14 per cent of the Mean.
5. Postatrioporal region 0·34–0·42 the length of the preatrioporal region: Mean 0·387: Standard Deviation 0·021: S.D. = 5·31 per cent of the Mean.
6. Myotomes from anterior end to atriopore 47–51: Mean 49·0: Standard Deviation 1·03: S.D. = 2·11 per cent of the Mean.
7. Myotomes from atriopore to anus 18–20: Mean 18·7: Standard Deviation 0·79: S.D. = 4·24 per cent of the Mean.
8. Myotomes posterior to anus 11–13: Mean 12·25: Standard Deviation 0·69: S.D. = 5·59 per cent of the Mean.
9. Total myotomes 77–84: Mean 80·0: Standard Deviation 1·57: S.D. = 1·96 per cent of the Mean.
10. Maximum length in sample examined 64 mm.; minimum length 25 mm.

The following characters not suitable for numerical evaluation assist in the recognition of this species and are illustrated in fig. 2 which has been prepared from *camera lucida* drawings of a small specimen from the sample. The dorsal fin is distinctly taller at the posterior end than in the anterior region. The rostrum is angular rather than curved in outline and there is no post-rostral notch. The caudal fin is moderately well developed and without subterminal indentations in outline. The anus is situated well before the centre of the lower lobe. In the preanal fin the lamina is greatly reduced and the fin chambers occupy almost the full width of the fin. The oral region is relatively small and the buccal cirri considerably shorter than in other species of the genus. There are, however, differences between large and small specimens in this sample which indicate that changes occur with growth in the relative height of the dorsal fin and in the number of preanal fin chambers. In specimens under 40 mm. in length the tallest of dorsal fin chambers are 4·0–6·0 times as high as broad (Mean 4·9) and the height of the dorsal fin is contained 7–10 times in the depth of the body in the mid-atrial region (Mean 8·4). In specimens over 40 mm. in length the tallest of dorsal fin chambers are only 2·7–3·5 times as high as broad (Mean 3·0) and the height of the dorsal fin is contained 10–12 times in the depth of the body in the mid-atrial region (Mean 10·7). It is evident, therefore, that the dorsal fin grows rapidly in height in the



BRANCHIOSTOMA ELONGATUM (PERUVIAN SAMPLE)

FIG. 2.

young animal and that the rate of increase in height of the fin becomes relatively slight as the animal approaches maturity. Increase in length of the body and hence of the dorsal fin, however, occurs without a corresponding increase in the number of dorsal fin chambers so that the proportions of the individual chambers alter with age. In the preanal fin, the number of fin chambers in specimens less than 40 mm. in length is 37–60 (Mean 52·6) whereas, in specimens over 40 mm. in length there are 62–80 chambers (Mean 69·2). There is no overlap in the numbers of preanal fin chambers between these two arbitrarily chosen groups of large and small specimens so that it is evident that the number of chambers must increase with the age of the animal. The changes in the relative height of the dorsal fin, the proportions of the dorsal fin chambers and the number of preanal fin chambers account for the very wide range of variation in these characters (characters 2, 3 and 4) in the diagnosis (where the figures are based on the entire sample) and consequently for the high value of the Standard Deviation evident when this is expressed as a percentage of the Mean. The occurrence of differential rates of growth in the dorsal fin and the body and the increase in number of preanal fin chambers with age appears to be a peculiarity of *B. elongatum* and has not been observed in other species of the genus.

Diagnosis of Branchiostoma elongatum *Sundevall* (*Galapagos sample*)

The following diagnosis is based on ten specimens taken by the Crossland Expedition from the Galapagos Islands on 25th July, 1924. They are part of a sample in the collection of the British Museum (Natural History), B.M. reg. nos. 1955. 12.13. 131–142. Counts and measurements have been made on these specimens and the results examined statistically.

1. Dorsal fin chambers number 356–420: Mean 383·6: Standard Deviation 21·21: S.D. = 5·53 per cent of the Mean.
2. Preanal fin chambers number 40–75: Mean 53·0: Standard Deviation 10·12: S.D. = 19·1 per cent of the Mean.
3. Tallest of dorsal fin chambers 4·0–7·0 times as high as broad: Mean 5·5: Standard Deviation 0·90: S.D. = 16·32 per cent of the Mean.
4. Height of dorsal fin contained 7–10 times in the depth of the body in the mid-atrial region: Mean 8·3: Standard Deviation 1·06: S.D. = 12·76 per cent of the Mean.
5. Postatrioporal region 0·33–0·41 the length of the preatrioporal region: Mean 0·36: Standard Deviation 0·029: S.D. = 8·18 per cent of the Mean.
6. Myotomes from anterior end to atriopore 47–50: Mean 48·9: Standard Deviation 1·0: S.D. = 2·05 per cent of the Mean.
7. Myotomes from atriopore to anus 17–19: Mean 18·3: Standard Deviation 0·67: S.D. = 3·69 per cent of the Mean.
8. Myotomes posterior to anus 9–11: Mean 10·1: Standard Deviation 0·88: S.D. = 8·73 per cent of the Mean.
9. Total myotomes 75–79: Mean 77·3: Standard Deviation 1·34: S.D. = 1·73 per cent of the Mean.
10. Maximum length in sample examined 29 mm.; minimum length 16 mm.

In general appearance the specimens of *B. elongatum* from the Galapagos Islands closely resemble those from Peru. As this sample, like that described by Snodgrass and Heller (1905), consists solely of small immature specimens, comparison of the shape and proportions of the fins and the number of preanal fin chambers can only be made with the smaller specimens in the Peruvian sample. It is not known whether changes in the proportions of the dorsal fin and in the number of preanal fin chambers occur in the Galapagos population of this species.

A comparison of the numerical characteristics of the Peruvian and Galapagos samples of *B. elongatum* is made in Table I where, for each of the characters numbered 1–9 in the diagnoses, the Mean and the Standard Deviation is given and from these '*t*' and hence '*P*', the degree of probability that such differences could occur between random samples of one population, have been calculated. In this table the Means and Standard Deviations are those given in the diagnoses of the two samples except for characters 2, 3 and 4 of the Peruvian sample where figures based on five specimens under 40 mm. in length have been substituted as offering a better comparison with the immature specimens of the Galapagos sample.

TABLE I

CHARACTER NUMBER	*B. elongatum* (Peruvian sample)		*B. elongatum* (Galapagos sample)		'*t*'	'*P*'
	MEAN	S.D.	MEAN	S.D.		
1	381·0	18·50	383·6	21·21	0·316	>0·25
2	52·6	9·64	53·0	10·12	0·068	>0·25
3	4·9	0·89	5·5	0·90	1·137	0·25
4	8·4	1·14	8·3	1·06	0·156	>0·25
5	0·387	0·021	0·36	0·029	2·638	0·02
6	49·0	1·03	48·9	1·0	0·234	>0·25
7	18·7	0·79	18·3	0·67	0·515	>0·25
8	12·25	0·69	10·1	0·88	6·666	<0·001
9	80·0	1·57	77·3	1·34	4·331	<0·001

A statistical analysis showing to what extent the differences between the Peruvian and the Galapagos samples of *B. elongatum* may be held to characterize the populations from which the samples were taken.

It is seen from Table I that the differences between the samples of *B. elongatum* from Peru and from the Galapagos Islands are not significant (assuming '*P*' = 0·05 to be the limit of significance) except in characters 5, 8 and 9. In character 5, the relative length of the postatrioporal region, the difference, although significant, is not great, but in character 8, the number of myotomes in the tail, the difference is highly significant. In accordance with the greater number of myotomes in the tail in the Peruvian lancelet there is also a significant difference in the total number of myotomes (character 9) in the two samples. Ignoring, therefore, the rather slight difference in the relative lengths of the postatrioporal region, it is clear that the only important feature distinguishing the lancelets of Lobos de Tierra and those of the Galapagos is the number of myotomes in the tail. The difference in this character is equivalent to the population differences found in *B. lanceolatum* from different regions (Webb, 1956b) and is insufficient to justify the recognition of the Galapagos lancelets as a distinct species. The comparison shows that the sample of *B. elongatum* from Peru can be considered representative of the species and, as it contains a number of mature specimens, it is more suitable for comparison with the Cape lancelet than the Galapagos form. A statistical analysis of the Peruvian sample of *B. elongatum* and the sample of *B. capense* is given in Table II.

Table II

CHARACTER NUMBER	*B. capense*		*B. elongatum* (Peruvian sample)		'*t*'	'*P*'
	MEAN	S.D.	MEAN	S.D.		
1	420·9	14·67	381·0	18·50	5·766	<0·001
2	71·2	6·11	64·0	10·35	1·994	0·05
3	4·55	0·64	3·6	1·03	2·616	0·02
4	9·4	1·36	10·0	1·41	1·061	0·25
5	0·405	0·014	0·387	0·021	2·394	0·02
6	46·0	1·26	49·0	1·03	6·524	<0·001
7	19·2	0.75	18·7	0·79	1·587	0·1
8	10·1	0·32	12·25	0·69	9·282	<0·001
9	75·3	1·45	80·0	1·57	7.586	<0·001

A statistical analysis showing to what extent the differences between *B. capense* and the Peruvian sample of *B. elongatum* may be held to characterize the populations from which the samples were taken.

In Table II the Means and Standard Deviations for each of the nine diagnostic characters of *B. capense* and the Peruvian sample of *B. elongatum* are given and from them '*t*' and hence '*P*' have been calculated to show how far the differences between the samples are significant. The chief characters in which the Cape lancelet differs from *B. elongatum* are the number of dorsal fin chambers (character 1), the number of myotomes before the atriopore (character 6) and the total number of myotomes (character 9) for each of which the value of '*t*' is high and that for '*P*' correspondingly low. Nevertheless in all of these characters the range of variation is such that there is some degree of overlap between the Cape sample and either the Peruvian or the Galapagos samples. Thus, on these characters alone, individual specimens of the Cape lancelet cannot necessarily be separated from specimens from one or other of the populations of *B. elongatum.* In the number of preanal fin chambers the Cape lancelet, with a rather higher number, is different from the Peruvian lancelet, but the difference is barely significant. In character 3, the proportions of the dorsal fin chambers, the Cape lancelet is not significantly different from the small specimens of the Peruvian lancelet although it is different from the mature forms. The height of the dorsal fin relative to the depth of the body (character 4) is a very variable character in all forms and differences between them are not significant. A difference in the relative length of the postatrioporal region exists in the two forms, but again it is barely significant. In character 7, the number of myotomes between the atriopore and the anus, there is a close similarity between the Cape lancelet and the Peruvian and Galapagos lancelets. In character 8, the number of myotomes in the tail, the Cape lancelet is significantly different from the Peruvian lancelet, but not from the Galapagos form.

Although, as would be expected, there is a greater difference between the Cape and the Peruvian than between the Peruvian and the Galapagos lancelets, on numerical characteristics alone the differences between any of the samples are not such that individual specimens from each are readily distinguishable. As the numerical characters do not provide a clear basis for separation, it is necessary to take into consideration other features not conveniently assessed on a numerical basis. From a comparison of figures 1 and 2, it is seen that the form of the rostrum and the oral region, the dorsal fin and also the caudal and preanal fins is quite different in the two lancelets. In general appearance *B. elongatum* has resemblances with *B. belcheri* whereas the Cape lancelet resembles the West African forms. Moreover, the changes in the proportions of the dorsal fin chambers, the relative height of the dorsal fin and the number of preanal fin chambers which occur in *B. elongatum* with advancing age are features not found in the Cape lancelet where the characters of large and small specimens do not differ significantly. The writer attaches considerable importance to these characters and, in view of the fact that the two forms can be separated by them, is of the opinion that the Cape lancelet should be regarded as a distinct form in which the similarity of numerical characteristics with *B. elongatum* is fortuitous.

The comparison of *B. capense* with the Indo-Pacific species *B. belcheri*, *B. bazarutense* and *B. arabiae* can be dismissed very briefly. In each of these three species the number of dorsal fin chambers is much fewer and the height of the dorsal fin relatively less than in *B. capense*. In consequence, the dorsal fin chambers are short and broad in these species, but long and narrow in *B. capense*. In *B. bazarutense* and *B. belcheri*, but not in *B. arabiae*, the postatrioporal region is relatively longer than in *B. capense*. An outstanding difference, however, lies in the number of myotomes before the atriopore which is much higher in *B. capense* than in the other three species. The difference in the number of anterior myotomes is also largely responsible for the clear difference in the total myotome number (see Webb, 1955 and 1956). Moreover the form of the rostrum, the oral region and the caudal and preanal fins in *B. capense* gives this lancelet a general appearance by which it can be distinguished immediately from the three Indo-Pacific species. It has already been pointed out that close relationships exist between *B. belcheri*, *B. bazarutense* and *B. arabiae* (see Webb, 1956) and it is evident that *B. capense* does not belong to this group.

Table III

CHARACTER NUMBER	*B. capense*		*B. nigeriense*		'*t*'	'*P*'
	MEAN	S.D.	MEAN	S.D.		
1	420·9	14·67	344·3	15·30	11·195	<0·001
2	71·2	6·11	53·9	3·07	7·548	<0·001
3	4·55	0·64	4·1	0·74	1·421	0·25
4	9·4	1·36	9·3	1·06	0·178	>0·25
5	0·405	0·014	0·417	0·030	1·134	0·25
6	46·0	1·26	41·7	1·70	6·298	<0·001
7	19·2	0·75	15·4	0·52	12·714	<0·001
8	10·1	0·32	10·9	0·57	3·816	0·001
9	75·3	1·45	67·9	1·45	11·110	<0·001

A statistical analysis showing to what extent the differences between samples of *B. capense* and *B. nigeriense* may be held to characterize the populations from which the samples were taken.

The only other species with which *B. capense* can be compared with profit are the West African species *B. africae*, *B. nigeriense*, *B. takoradii and B. leonense* which form a closely related group from the Guinea Coast (see Webb 1955, 1956a and 1956b). It is worth noting that, in describing *B. africae*, Hubbs (1927) compared this species with *B. californiense*, *B. capense*, *B. lanceolatum* and *B. tattersalli* thus evidently recognizing a degree of relationship between *B. capense* and *B. africae*. Unfortunately specimens of *B. africae* from which a statistical analysis of the species can be prepared are not available. However *B. nigeriense* is a species very close to *B. africae* and for which there is an abundance of material. *B. nigeriense* occurs in two forms, one from the sea and the other from brackish water. An analysis of the marine form has already been published (Webb, 1956a) and these figures are here compared with those for *B. capense* in Table III. A detailed comparison of *B. capense* with *B. takoradii* and *B. leonense* is considered unnecessary in view of the close relationship existing between all the Guinea Coast lancelets.

In Table III, for each of the characters numbered 1–9 in the diagnoses for *B. capense* and *B. nigeriense*, the Mean and the Standard Deviation is given and from these '*t*' and hence '*P*' have been calculated as a measure of the extent of the differences between the samples. High values for '*t*' and correspondingly low values for '*P*' show that *B. capense* and *B. nigeriense* are significantly different in all characters except the height of the dorsal fin, the proportions of the dorsal fin chambers and the relative length of the postatrioporal region (characters 4, 3 and 5 respectively). In some characters (the number of preanal chambers, the number of myotomes before the anus and the total myotome number) the difference between the two samples is considerable. In the number of myotomes in the tail (character 8), however, it is not so great and in the number of dorsal fin chambers (character 1) there is a tendency among the Guinea Coast lancelets for this to be high, 400 chambers occasionally being exceeded in *B. leonense*. With regard to characters other than those treated numerically, it has already been mentioned that there is a striking similarity between the form of the rostrum, the oral region and the caudal fin in *B. capense* and that in *B. nigeriense* and *B. leonense*. In general appearance *B. capense* can be mistaken for *B. nigeriense* except for a difference in number and length of the preanal fin chambers. It seems, therefore, that these two lancelets possess a considerable number of identical characters which strongly suggests that they have diverged from a common stock. Thus, whereas there is no doubt that *B. capense* is distinct from the Guinea Coast lancelets, it is also evident that it is an extreme member of that series and is more closely related to *B. nigeriense* or perhaps *B. africae* than to any other known species. Lancelets have not yet been recorded from the coasts of French Equatorial Africa, Angola, or South West Africa where forms intermediate between *B. capense* and the Tropical West African species might be expected to occur. The proposed relationship between *B. capense* and the West African lancelets is in accordance with their geographical location and supports the contention that *B. capense* has no close affinities with *B. elongatum* in spite of the remarkable agreement between their numerical characteristics. The view, therefore, is taken that *B. capense* is a valid species not to be confused with the lancelets of the western seaboard of the Americas.

Branchiostoma belcheri (Gray)

Amphioxus belcheri Gray (1847)

Branchiostoma belcheri Gray (1851)

(for a full list of references see Franz, 1922, and Hubbs, 1922).

Material examined. Nine specimens (MOR. 43. K. 20.1.54) dredged at Linga-linga, Morrumbene Estuary, Portuguese East Africa, common on a sandy bottom. One specimen (P.E.A. 14S. –.11.55) dredged off Mozambique Island, Portuguese East Africa. These specimens are deposited in the Department of Zoology, University of Cape Town.

Distribution. Coasts of Borneo, China and Japan, Singapore, Philippine Islands, Torres Strait, Madras, Ceylon and East Africa.

Remarks. The nine specimens from Linga-linga are a uniform series, but the specimen from Mozambique Island shows minor differences from these. It has therefore been considered desirable to give a separate diagnosis for each sample.

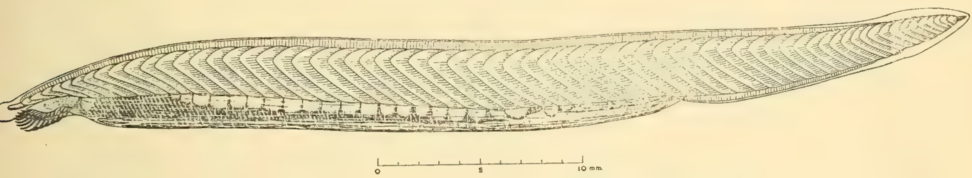
Diagnosis of the Linga-linga lancelet. In the following diagnosis counts and measurements have been made on the 9 specimens in this sample and the results have been analysed statistically.

1. Dorsal fin chambers number 258–306: Mean 287·0: Standard Deviation 15·1: S.D. = 5·26 per cent of the Mean.
2. Preanal fin chambers number 70–88: Mean 80·6: Standard Deviation 5·61: S.D. = 6·96 per cent of the Mean.
3. Tallest of dorsal fin chambers 3·0–3·6 times as high as broad: Mean 3·17: Standard Deviation 0·24: S.D. = 7·48 per cent of the Mean.
4. Height of the dorsal fin contained 7–10 times in the depth of the body in the mid-atrial region: Mean 8·8: Standard Deviation 0·97: S.D. = 11·05 per cent of the Mean.
5. Postatrioporal region 0.43–0·47 the length of the preatrioporal region: Mean 0·450: Standard Deviation 0·012: S.D. = 2·72 per cent of the Mean.
6. Myotomes from anterior end to atriopore 36–39: Mean 37·1: Standard Deviation 0·79: S.D. = 2·13 per cent of the Mean.
7. Myotomes from atriopore to anus 17–19: Mean 17·7: Standard Deviation 0·71: S.D. = 4·0 per cent of the Mean.
8. Myotomes posterior to anus 9–11: Mean 9·9: Standard Deviation 0·60: S.D. = 6·07 per cent of the Mean.
9. Total myotomes 63–66: Mean 64·7: Standard Deviation 1·12: S.D. = 1·73 per cent of the Mean.
10. Maximum length in sample examined 48 mm.; minimum length 42 mm.

Diagnosis of the Mozambique Island lancelet.

1. Dorsal fin chambers number 276.
2. Preanal fin chambers number 68.
3. Tallest of dorsal fin chambers 4·0 times as high as broad.
4. Height of the dorsal fin contained 8 times in the depth of the body in the mid-atrial region.
5. Postatrioporal region 0·46 the length of the preatrioporal region.
6. Myotomes from anterior end to atriopore 34.
7. Myotomes from atriopore to anus 17.
8. Myotomes posterior to anus 11.
9. Total myotomes 62.
10. Length of specimen 62 mm.

The following characters also assist in the recognition of this species and are illustrated in fig. 3 which has been prepared from *camera lucida* drawings of the Linga-linga lancelet. The rostrum is of moderate size and is separated from the dorsal fin by a post-rostral notch. The comparatively low dorsal fin is of approximately the same height throughout the length of the body. The caudal fin is rather small and lacks the subterminal indentations in outline present in *B. capense*. The anus is situated in advance of the centre of the lower lobe of the caudal fin. The preanal fin is long but comparatively narrow and the preanal chambers extend almost the full width of the fin. Seen from the ventral aspect the preanal fin chambers are broad and, in some specimens, there is incipient doubling of the fin either at the anterior end only or throughout its entire length. The presence of a double preanal fin has been mentioned by Gilchrist (1923) as a character of *B. bazarutense*. The anterior end of the body is slender and the oral hood comparatively shallow dorso-ventrally. In all the specimens examined well-formed gonads were present. The body is more or less circular in cross-section in contrast with the marked lateral flattening of most species other than *B. belcheri*.



BRANCHIOSTOMA BELCHERI (PORTUGUESE EAST AFRICAN SAMPLE)

FIG. 3.

These Portuguese East African lancelets agree in all characters with *B. belcheri* and do not differ very greatly from *B. bazarutense*. The occurrence of *B. belcheri* on the coast of East Africa is of special interest as this species seems to be predominantly an Asiatic form. It has already been mentioned that Franz (1922) recorded *B. belcheri* from a locality near Zanzibar, but that this record badly needed confirmation. The present collection from Linga-linga and Mozambique Island provides that confirmation and suggests that *B. belcheri* is probably well established on the East African coast as a distinct population. To determine how far the East African form differs from the Asiatic members of *B. belcheri*, a comparison is made between the Linga-linga sample and another from Amoy on the coast of China, a statistical analysis of which has already been published (Webb, 1956). In Table IV, from the Means and the Standard Deviations for the nine diagnostic characters of the Linga-linga and Amoy lancelets, 't' and hence 'P' has been calculated to show how far the samples may be considered representative of distinct populations. It is clear from the low values of 't' and the high values for 'P' obtained, that the Linga-linga and the Amoy lancelets are not significantly different except in the number of dorsal fin chambers, the relative length of the postatrioporal region and the number of myotomes between the atriopore and the anus (characters 1, 5 and 7). Moreover in only one of these three characters, the relative length of the postatrioporal region of the body, can the difference between the samples be considered highly significant. The measure of agreement, therefore, is greater between the Linga-linga samples than has been shown to exist between samples of *B. lanceolatum* taken from Naples, Plymouth and the Kattegat (Webb, 1956b). In general appearance, also, the Linga-linga lancelet and the Amoy lancelet are almost identical (compare fig. 3 with Webb, 1956, fig. 2). There is no longer any doubt, therefore, that *B. belcheri* is represented in East Africa, although there are population differences between the East African and the Asiatic forms.

TABLE IV

CHARACTER NUMBER	Linga-linga lancelet		Amoy lancelet		't'	'P'
	MEAN	S.D.	MEAN	S.D.		
1	287·0	15·10	305·0	23·64	2·130	<0·05
2	80·6	5·61	78·1	5·26	1·165	0·25
3	3·17	0·24	2·96	0·31	1·788	0·1
4	8·8	0·97	9·08	0·96	0·726	>0·25
5	0·45	0·012	0·50	0·024	5·808	<0·001
6	37·1	0·79	36·5	0·82	1·844	0·1
7	17·7	0·71	17·0	0·76	2·339	>0·02
8	9·9	0·60	10·0	0·54	0·448	>0·25
9	64·7	1·12	63·56	1·00	2·746	0·01

A statistical analysis showing to what extent the differences between samples of *B. belcheri* from Linga-linga in Portuguese East Africa and Amoy in China may be held to characterize the populations from which the samples were taken.

The single specimen from Mozambique Island has been shown to differ from those from Linga-linga more particularly in the rather low number of myotomes before the atriopore. Whereas it is impossible to draw any conclusions from such differences in a single specimen, the occurrence of this specimen does suggest that there might be other populations of *B. belcheri* on the East African coast where isolation may have given rise to slight differences which are maintained. It is also possible that Gilchrist's species *B. bazarutense* should more properly be referred to as a variant of *B. belcheri*. In his description of *B. bazarutense* Gilchrist was more concerned with separating his species from *B. capense* and *B. elongatum* than any other species, and he overlooked the similarity with *B. belcheri*, the existence on the East African coast of this species not being suspected at that time. Gilchrist placed some weight on the peculiar form of the preanal fin in *B. bazarutense*, but the approach to a similar condition in the Linga-linga lancelet shows that this character is, in fact, a further link with *B. belcheri.* Nevertheless *B. bazarutense* can be recognized from a number of slight differences which involve most of the characters, but whether these differences are sufficient to warrant specific recognition is another matter which, as the types of this species appear to have been lost, can only be settled when a new sample has been obtained.

Branchiostoma lanceolatum (Pallas)

Limax lanceolatus Pallas (1774)

Branchiostoma lubricus Costa (1834)

Amphioxus lanceolatus Yarrell (1836)

Branchiostoma lanceolatum Gray (1851)

Material examined. Two specimens (MOR. 43.K. 20.1.54) dredged at Linga-linga, Morrumbene Estuary, Portuguese East Africa, from sandy bottom. These specimens are deposited in the Department of Zoology, University of Cape Town.

Distribution. Norwegian coast, North Sea, Kattegat, Heligoland, English Channel, Irish Sea, Mediterranean Sea, Suez Canal, Arabian Sea, Madagascar, Portuguese East Africa.

Remarks. These two specimens of *B. lanceolatum* were included in the same sample as the nine specimens of *B. belcheri* from Linga-linga, Portuguese East Africa. Apparently the two species have been taken from the same locality at the same time.

Diagnosis of the Portuguese East African sample of Branchiostoma lanceolatum

1. Dorsal fin chambers number 270 and 280.
2. Preanal fin chambers number 32 and 34.
3. Tallest of dorsal fin chambers 2·5 times as high as broad.
4. Height of dorsal fin contained 11 and 12 times in the depth of the body in the mid-atrial region.
5. Postatrioporal region 0·40 and 0·42 times the length of the preatrioporal region.
6. Myotomes from anterior end to atriopore 34 and 35.
7. Myotomes from atriopore to anus 13.
8. Myotomes posterior to anus 10.
9. Total myotomes 57 and 58.
10. Length of the specimens examined 31 mm.

The two specimens examined were not in a very good condition, but, as far as could be determined, in general appearance and in the form of the rostrum and the caudal fin they resembled *B. lanceolatum* from the central Mediterranean region (see Webb, 1956b).

This is the third record of *B. lanceolatum* from a region east of the Suez Canal where this species is said to occur in abundance (Gruvel, 1933). Prenant (1928) first recorded lancelets which he held to be *B. lanceolatum* from the north-west coast of Madagascar. In 1933 the 'John Murray' Expedition collected a single specimen of the species in a haul containing a large number of *B. arabiae* (Webb, 1956). The present record from Portuguese East Africa is similar in that the two specimens were taken together with another species, but this time *B. belcheri*. This sporadic occurrence of *B. lanceolatum* outside European waters suggests that this species is spreading from the Suez Canal to the Arabian Sea and Indian Ocean.

TABLE V

CHARACTER NUMBER	Range of variation in Indian Ocean and Arabian Sea samples of *B. lanceolatum*			Total range of variation in European samples of *B. lanceolatum*
	Portuguese East Africa	Madagascar	Arabia	
1	270–280	220–280	264	200–270
2	32–34	35	47	29–48
3	2·5	—	1·6	1·4–2·7
4	11–12	—	12	8–16
5	0·40–0·42	—	0·52	0·38–0·51
6	34–35	35	37	33–38
7	13	15	13	12–16
8	10	12	14	10–14
9	57–58	62	64	58–65

A comparison of the recorded range in variation of the numerical diagnostic characters in the Indian Ocean and Arabian Sea samples of *B. lanceolatum* with the total range in variation in the European samples of that species.

In Table V the diagnoses for the Portuguese East African, Madagascan and Arabian samples of *B. lanceolatum* are compared with that of the European samples of the species. It is seen that the total range in variation in each character in the European samples covers the range for the Indian Ocean and Arabian Sea forms with very few exceptions. These exceptions are a rather high number of dorsal fin chambers in the Portuguese East African and the Madagascan samples (character 1), the relatively long postatrioporal region in the Arabian specimen (character 5) and a low total number of myotomes in one of the Portuguese East African specimens (character 9). In each case, however, these figures fall outside the European range by so little that it is doubtful how far they can be considered significant. Two facts emerge from this comparison which may be of value. First the diagnoses for the Indian Ocean and Arabian Sea samples do not conform to any of the populations of the European lancelet for which detailed figures are available (Webb, 1956b). They may be similar, however, to the Suez Canal population a diagnosis for which has not been published. Second, the numerical range shown by the characters of the three samples from East of the Suez Canal, when taken together, exceeds in certain respects that of any of the European populations determined from larger samples. The probability is, therefore, that the Portuguese East African, Madagascan and Arabian samples are not all taken from the same population. The first two of these samples probably belong to one population, taking into account both the similarity of the diagnoses and their geographical location, but the Arabian specimen almost certainly belongs to another. On the assumption that the populations of *B. lanceolatum* in the Indian Ocean and Arabian Sea have been derived from the eastern Mediterranean population at a time subsequent to the opening of the Suez Canal in 1869, it can be presumed that any differences between populations in the Indian Ocean and in the Arabian Sea have arisen during a period of about sixty years. It is known that the English Channel population of *B. lanceolatum* has remained stable for more than seventy years (Webb, 1956b), so that any changes that may have occurred in the eastern Mediterranean lancelets since their migration through the Red Sea may be due either to the change in environmental conditions accompanied by isolation or to some degree of hybridization with the endemic lancelets. In the Arabian Sea *B. lanceolatum* is sympatric with *B. arabiae* and in Portuguese East Africa with *B. belcheri*. Hybridization with *B. arabiae* might account for rather higher numbers of dorsal and preanal fin chambers than are commonly found in lancelets at Naples, but not, perhaps, for the relatively long postatrioporal region. Similarly, hybridization with *B. belcheri* could account for a high dorsal fin chamber number and a rather tall dorsal fin. The evidence, however, is not at all clear and further samples of *B. lanceolatum* from Portuguese East Africa, the Arabian Sea and, in particular, the Suez Canal are required before an opinion can be given.

Conclusions

An examination of the types of *Branchiostoma capense* and new collections from South Africa of this species has been made. It is concluded that *B. capense* is a valid species and is not synonymous with *B. californiense* or *B. elongatum* as has been proposed by Tattersall (1903) and Franz (1922, 1922a and 1930). The remarkable similarity between many of the characters of *B. capense* and *B. elongatum* is thought to be due to convergence and not to close affinity of these geographically widely separated forms. Comparisons have been made between *B. capense* and the neighbouring species *B. belcheri*, *B. bazarutense* and *B. arabiae* from the east coast of the African continent and *B. africae*, *B. nigeriense*, *B. takoradii* and *B. leonense* from West Africa. *B. capense* has been shown to be related to the Guinea Coast lancelets of West Africa and to be an extreme member of that series. The Cape lancelet extends in range from the south-west tip of the Cape Province (Simons Bay and False Bay) eastward to Port Elizabeth (Algoa Bay).

On the east coast of Africa a different species, *B. belcheri*, is established and has been recorded from the Morrumbene Estuary and Mozambique Island in Portuguese East Africa and also by Franz (1922) from a locality near Zanzibar. The population of *B. belcheri* at the Morrumbene Estuary is very similar to that at Amoy on the China coast and the two forms can only be distinguished by minor differences. *B. bazarutense*, described by Gilchrist (1923) from the Bazaruto Islands off Portuguese East Africa, is a close relative of *B. belcheri* differing from the Morrumbene form, but not, perhaps, sufficiently to warrant specific distinction. Another species, *B. arabiae*, which is related to *B. belcheri*, has been described by Webb (1956) from the Arabian coast. Sympatric with *B. arabiae* and *B. belcheri* from the Morrumbene Estuary are populations of *B. lanceolatum* which have evidently been derived from a Suez Canal population of that species. A further record of *B. lanceolatum* has also been made by Prenant (1928) from the north-west coast of Madagascar.

The lancelets of South and East Africa, therefore, appear to have been derived from several different sources and consequently do not form a closely related group as, for instance, seems to be the case with the lancelets of the west Atlantic or, to a lesser extent, those of the east Atlantic. An explanation of the occurrence of such a variety of different lancelets on these coasts is probably to be found in the pattern of currents in the Indian Ocean. *B. capense*, being related to the lancelets of the west side of the continent, is probably endemic. Its distribution seems to be limited to a region of the Cape coast just beyond the reach of the south-west warm Agulhas Current which is formed from components from the north-south Mozambique Current, running between Madagascar and Portuguese East Africa, and the east-west Equatorial Current from Australia to the south of Madagascar. The direction of flow of the Agulhas Current may well prove a barrier to the spread of the planktonic larvae of *B. capense* northward beyond Port Elizabeth. The reason for the abrupt termination of the range of this species to the west at the Cape (Simons Bay and False Bay) might be due to the presence of the cold water of the Benguela Current which originates south of this point and passes up the west coast of the continent. The Benguela Current, however, provides a connection between the Cape and the Guinea Coast of tropical West Africa which could account for a relationship between *B. capense* and the Guinea Coast lancelets as there must be some intermixing of waters between the Benguela and the

Guinea Coast Current at the level of the equator. From the direction of flow of the Benguela Current it would seem more likely that the Guinea Coast lancelets are derived from the Cape lancelet than that the reverse is true.

B. belcheri, which is an Asiatic form common in the China Seas, East Indies and North Australia, appears to have been carried to East Africa by the broad east-west Equatorial Current which strikes the east coast of Madagascar and turns both to the north and to the south, passing around the island. The direction of flow of this current could account for the occurrence of *B. belcheri* at Zanzibar and in Portuguese East Africa, and, perhaps, elsewhere on the East African coast north of Port Elizabeth. This species should also occur in Madagascar. The close similarity between the East African and the Amoy forms of *B. belcheri* suggests that a migration from east to west in the Equatorial Current is made with some frequency and that the East African populations are not fully isolated from the Asiatic. *B. arabiae* is connected with the East African population of *B. belcheri* by the seasonal north-east Monsoon Drift, but has come to occupy a somewhat isolated position on the Arabian coast at the entrance to the Gulf of Oman. *B. bazarutense* similarly has only been recorded once from the Bazaruto Islands. Both of these forms have evidently been derived from *B. belcheri* and presumably could only have arisen through occupation of an isolated area. There must, therefore, be regions along the East African coast where such isolation is possible.

The mode of distribution of *B. lanceolatum* in the Arabian Sea and Indian Ocean can be similarly explained. Once the species reached the Gulf of Aden from Suez by means of the reciprocal currents of the Red Sea, one current runs along the coast of Somaliland to meet the seasonal south-west Monsoon Drift passing the East African coast to Madagascar and the Mozambique Current, while another runs north-east along the Arabian coast. Thus the south-west Monsoon Drift could account for the presence of *B. lanceolatum* on the north-west coast of Madagascar and in Portuguese East Africa, and the Arabian Current for the presence of that species in the locality of *B. arabiae*. The distribution of lancelets on the East African coast, therefore, is in accordance with the ocean currents, and may give an indication of the geographical range of other marine organisms similarly distributed by means of planktonic larvae in the Indian Ocean.

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